

THERMAL BEHAVIOUR OF POLAR FISH: A BRIEF SURVEY AND SUGGESTIONS FOR RESEARCH *

by

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ABSTRACT. - Temperature is considered to be the most pervasive environmental factor that limits the temporal and spatial distribution, and governs the migratory behaviour, of marine fish. Thermal behaviour in fish has been studied widely but the underlying components that affect temperature selection are still poorly understood. Further, very little attention has been drawn to the study of thermal behaviour in polar fish. This paper intends to: (1) provide a brief overview of nonthermal components that may be linked to temperature selection in fish, (2) outline the rationale behind a current project on biological correlates of selected temperature in two Arctic marine fish species, the capelin (*Mallotus villosus*) and the polar cod (*Boreogadus saida*), and (3) present some preliminary results obtained from laboratory experiments using an electronic shuttle-box system.

RÉSUMÉ. - Comportement thermique des poissons polaires: bilan et perspective des recherches.

La température est considérée comme le facteur de l'environnement le plus important pour limiter la distribution spatiale et temporelle et régir le comportement migratoire des poissons marins. Le comportement des poissons en fonction de la température a largement été étudié, mais les raisons profondes de la sélection due à la température sont encore mal comprises. De plus, l'attention a été très peu attirée par l'étude du comportement thermique chez les poissons polaires. Cette note a pour but: (1) de donner un bref aperçu des facteurs autres que la température mais liés à cette dernière et qui agissent sur le comportement des poissons, (2) de souligner les objectifs d'un projet de recherche sur le rôle de la température chez deux espèces de poissons marins arctiques, le capelan (*Mallotus villosus*) et la morue arctique (*Boreogadus saida*), et (3) présenter quelques résultats préliminaires obtenus au cours d'expérimentations en laboratoire au moyen d'une chambre d'élevage équipée d'enregistreurs électroniques.

Key-words. - Gadidae, *Boreogadus saida*, Osmeridae, *Mallotus villosus*, Polar Fish, PN, Arctic Ocean, Temperature selection.

Mathematical models are presently being developed to evaluate potential effects of global climate change on Arctic marine environments and biota (e.g. Johannessen *et al.*, 1995; Fortier *et al.*, 1996). Models of this kind need inputs concerning the basic biological processes that take place in the Arctic and how these processes are affected by environmental changes of natural and anthropogenic origin. Temperature is considered to

* This paper was presented at the 3rd Workshop of the European Science Foundation Network on "Antarctic Fish: Ecology, lifestyle and adaptative evolution. Comparison with Arctic fish", Saint-Rémy-lès-Chevreuse, 13-14 September, 1996.

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be the most pervasive environmental factor that limits the temporal and spatial distribution, and governs the migratory behaviour of marine fish and other aquatic ectotherms (Harden Jones, 1968; Neill, 1979; Coutant, 1987; Jakobsson and Østvedt, 1996). Thus, the main purpose of this paper is to: (1) provide a brief overview of the nonthermal components that may be linked to temperature selection in fish and (2) outline the rationale and objectives behind a current project on biological correlates of selected temperature in capelin (*Mallotus villosus*) and polar cod (*Boreogadus saida*). Both species have a key-role in Arctic marine ecosystems and any change in their distribution and migratory behaviour may have profound ecological consequences and, thereby, affect high latitude fisheries.

THERMAL BEHAVIOUR IN FISH

A bulk of literature has addressed sundry aspects of temperature selection in fish. Temperature preference data have been compiled by e.g., Ivlev and Leyzerovich (1960), Coutant (1977), and Jobling (1981), and much information can be extracted from the following symposia: "Temperature preference studies in environmental impact assessments: an overview with procedural recommendations" (*J. Fish. Res. Board Can.*, vol. 34, 1977); "Thermoregulation in ectotherms" (*Amer. Zool.*, vol. 19, 1979); and "From environment to fish to fisheries: a tribute to F. E. J. Fry" (*Trans. Amer. Fish. Soc.*, vol. 119, 1990).

Temperature selection and the "final thermal preferendum" paradigm

With a few exceptions, fish are not physiologically equipped to maintain a body temperature that differs substantially from that of the environment (Stevens and Fry, 1974; Cossins and Bowler, 1987, and references therein; Christiansen *et al.*, 1991). Although the body temperature of fish varies in accord with that of the surrounding water this does not necessarily imply that fish are incapable of responding to the prevailing temperature regimes.

Fish may discriminate temperature differences as small as 0.03°C (Bull, 1936), and when exposed to a thermal gradient or a free-choice situation they tend to congregate within narrow thermal zones by altering their spatial distribution and migratory pattern. Thus, fish display behavioural thermoregulation expressed via preference and avoidance responses. Short-term or acute temperature selection in fish may be affected by the temperature to which the fish have been acclimated (*in sensu* Clarke, 1991), often in a nonlinear manner, ranging from direct to inverse proportionality (Hutchison and Maness, 1979; Kelsch and Neill, 1990). Contrary to acute thermal selection, long-term or final thermal preferenda in fish (usually selected > 24 hours after placement in a thermal gradient) are believed not to be influenced by previously experienced temperatures. Several studies of fish have shown that the final preferendum correlates well with the temperature where growth and physiological performance of the species is optimized (Jobling, 1981, 1995). The final preferendum may, thus, be a species-specific characteristic which is reflected in the zoogeographic and temporal distribution; i.e. the "final thermal preferendum" paradigm (Fry, 1947; Reynolds and Casterlin, 1979). However, the duration of the temperature acclimation period preceding studies of final preferenda is deemed to be important, and, to our knowledge, no study has examined the intra-specific final thermal preferendum in groups of fish which have experienced different temperature regimes throughout their entire life-span.

Temperature selection and high-temperature tolerance in polar fish

One of the most conspicuous and well studied features of polar fish is their ability to withstand temperatures close to the freezing point of seawater (e.g., DeVries, 1988). By contrast, the literature dealing with high-temperature tolerance in polar fish is sparse and often inconsistent especially at the organismic level.

Organisms living in temperature fluctuating environments tend to have a greater capability to adjust to high-temperature events than those organisms that inhabit more temperature-stable environments (Hoffmann, 1995). Indeed, several of the Antarctic notothenioid species are constantly subjected to sub-zero temperatures (Clarke and Johnston, 1996); they appear to be extremely stenothermal (Somero, 1991) and, when acutely exposed (Genus *Trematomus*), they succumb at temperatures above approximately 6°C (Somero and DeVries, 1967). On the other hand, when subjected to a gradual increase in ambient temperature (0–10°C; 1°C hour⁻¹), notothenioids displayed behavioural and respiratory changes but did not die. Moreover, all species examined recovered perfectly as temperature was restored at 0°C (Fanta *et al.*, 1989). Although having evolved under extremely cold and temperature-stable conditions, Antarctic fish are capable of expressing heat-shock proteins which are believed to counteract the deleterious effects of high temperatures (Maresca *et al.*, 1988; Coleman *et al.*, 1995). Further, they detect temperature differences (Crawshaw and Hammel, 1971) and display a consistent preference for seawater close to freezing (*Pagothenia borchgrevinki*; -1.8°C) when placed in a thermal gradient (Macdonald *et al.*, 1987).

A high Arctic fish species such as the polar cod inhabits ice-covered, sub-zero waters for most of the year (Ponomarenko, 1968; Christiansen, 1995a) but, in contrast to its Antarctic counterparts, polar cod have been held at laboratory temperatures up to 14°C for several weeks with no signs of distress (Christiansen, 1995b). This is a temperature which polar cod will never encounter in its natural environment (Ponomarenko, 1968; Schurmann and Christiansen, 1995). Further, when polar cod are being held under laboratory conditions they appear to select temperatures well above those experienced in the wild (Schurmann and Christiansen, 1994). Final preferenda obtained from laboratory experiments are often higher than the temperature regimes observed among fish in nature (Reynolds, 1977). The apparent discrepancy between fundamental and realized thermal niches (*in sensu* Magnuson *et al.*, 1979) may, therefore, be due to the effect of various nonthermal stimuli. Thus, it seems that the concept of stenothermality in polar fish, particularly at the organismic level, may need further examination.

The underlying determinants of temperature selection

The temperature zone selected by fish under natural conditions is thought to be affected by their acclimatization state (*sensu* Clarke, 1991) resulting from the interaction of a host of environmental, ecological and physiological variables (Beitinger and Fitzpatrick, 1979; Reynolds and Casterlin, 1979). Information on some relevant nonthermal components that may affect temperature selection has been extracted from the published literature and is compiled in table I.

Several different approaches and experimental devices have been employed (Ivlev, 1960, 1962), and this may confound comparisons of results from different studies (Table I). Final thermal preferenda have been determined either from (a) short-term (within a few hours) temperature selection in fish acclimated to a series of different temperatures, to determine the relationship between acute preference and acclimation temperatu-

Table 1. - A compilation of some biological and environmental components that may affect temperature selection in fish. Although far from complete, some generalizations may be drawn from the table. For example, low levels of dissolved oxygen (hypoxia) result in a consistent selection for lower temperatures irrespective of species, whereas e.g. food availability and nutritional state appear to elicit species-specific temperature responses. M = marine; FW = fresh water; ANA = anadromous; CAT = catadromous; FTS = final thermal selection; ATS = acute thermal selection; native habitat according to Nelson, 1984.

Nonthermal components	Species	Native habitat*	Selected temperature	Methodology	Miscellaneous	Study
Biological:						
Social interactions	<i>Pomadasys commersonnii</i>	M-Atlantic, Indian	Not affected	FTS-Horizontal gradient	Different group sizes	Deacon & Hecht 1995
	<i>Lepomis macrochirus</i>	FW-North America	Affected	FTS-Shuttle-box	Juvenile with/without adult	Beitinger & Magnuson 1975
Body size	<i>Gambusia nobilis</i> and <i>Cyprinodon elegans</i>	FW-The Americas	Affected	Horizontal gradient	Alone vs together	Gehlbach <i>et al.</i> 1978
	<i>Lepomis macrochirus</i>	FW-North America	Not affected	FTS-Shuttle-box	Various body lengths	Beitinger & Magnuson 1975
Age	<i>Oncorhynchus mykiss</i>	ANA-Northern hemisphere	Lower in older fish	ATS-Vertical gradient	Age 1-12 months	Kwain & McCauley 1978
	<i>Idalurus natalis</i>	FW-North America	Lower in older fish	FTS-Shuttle-box	Juvenile vs adult	Reynolds & Casterlin 1978
	<i>Morone saxatilis</i>	FW-North America, Europe, North Africa	Lower in older fish	Radiotracer/field		Coutant 1987
	<i>Cymatogaster aggregata</i>	M-North Pacific	Lower in neonate fish	ATS-Horizontal gradient/field	Lower in laboratory than in field	Shrode <i>et al.</i> 1983
	<i>Gadus morhua</i>	M-Atlantic, Arctic	Lower in older fish	FTS-Horizontal gradient	Age 1-3 years	Tatankin 1972
Food availability and nutritional state	<i>Pollachius virens</i>	M-Atlantic	Lower in older fish	FTS-Horizontal gradient	Age 1-3 years	Tatankin 1972
	<i>Lota lota</i>	FW-North America, Eurasia	Lower in younger larvae	ATS-Horizontal gradient	Age 2-30 days	Evropceva 1944
	<i>Salvelinus namaycush</i>	FW-Northern hemisphere	Lower in starved fish	FTS-Shuttle-box	Juveniles	Mac 1985
	<i>Salvelinus fontinalis</i>	ANA-Northern hemisphere	Lower in starved fish	FTS-Horizontal gradient	Fingerlings	Javadi & Anderson 1967
	<i>Oncorhynchus mykiss</i>	ANA-Northern hemisphere	Not affected	FTS-Shuttle-box	Single observation	Schurmann <i>et al.</i> 1991
Sex	<i>Oncorhynchus nerka</i>	ANA-Northern hemisphere	Lower in post-feeding fish	Field observations	Limited food availability	Brett 1971
	<i>Salmo salar</i>	ANA-Northern hemisphere	Higher in starved fish	FTS-Horizontal gradient	Fingerlings	Javadi & Anderson 1967
	<i>Oreochromis mossambicus</i>	FW-Africa	Higher in starved fish	ATS-Horizontal gradient	Mortality amongst starved fish	Boltz <i>et al.</i> 1987
	<i>Hippoglossoides platessoides</i>	M-Arctic, Atlantic	Lower in starved fish	FTS-Horizontal gradient		Morgan 1993
	<i>Cottus extensus</i>	FW-Northern hemisphere	Higher in post-feeding fish	Trawls/field and laboratory	Ad libitum food during day	Wurtsbaugh & Neverman 1988
Sex	<i>Pomatomus saltatrix</i>	M-Atlantic	Affected	ATS-Vertical gradient	Juveniles	Olla <i>et al.</i> 1985
	<i>Salmo trutta</i>	ANA-Northern hemisphere	Higher in female fish	Radiotracer/field		Spigorelli <i>et al.</i> 1983
	<i>Salmo trutta</i>	ANA-Northern hemisphere	Higher in male fish	Radiotracer/field	Adults in late summer	Spigorelli <i>et al.</i> 1983
	<i>Pocilia reticulata</i>	FW-The Americas	Lower in male fish	ATS-Horizontal gradient	Male fish alone	Johansen 1985
	<i>Pocilia reticulata</i>	FW-The Americas	Same in male and female fish	ATS-Horizontal gradient	Male and female fish together	Johansen 1985

Table 1. - Continued.

Nonthermal components	Species	Native habitat*	Selected temperature	Methodology	Miscellaneous	Study
Sexual maturation	<i>Oncorhynchus tshawytscha</i> <i>Anguilla rostrata</i> <i>Mallotus villosus</i>	ANA-Northern hemisphere CAT-North Atlantic M-Northern hemisphere	Higher Not affected Higher	Radiotransmitter/field FTS-Horizontal gradient Field surveys	Thermal refuges FTS highly variable	Berman & Quinn 1991 Haro 1991 Shackell <i>et al.</i> 1994
Hybridization	<i>Salmo</i> and <i>Salvelinus</i>	ANA-Northern hemisphere	Affected	ATS-Horizontal/vertical gradients	Fry and fingerlings	Peterson <i>et al.</i> 1979
Bacterial pyrogens	<i>Lepomis macrochirus</i>	FW-North America	Higher	FTS-Shuttle-box	Fever	Reynolds & Casterlin 1979
Environmental:						
Salinity	<i>Cichlasoma urophthalmus</i> <i>Pomadasys commersonnii</i>	FW-Central and South America M-Atlantic, Indian	Higher at 15 ppt; lower at 30 ppt Not affected	ATS-Horizontal gradient FTS-Horizontal gradient	Euryhaline (0, 15, and 30 ppt) Euryhaline	Stauffer & Boltz 1994 Deacon & Hecht 1995
Hypoxia	<i>Gadus morhua</i> <i>Oncorhynchus mykiss</i> <i>Hydrogobius placatus</i>	M-Atlantic, Arctic ANA-Northern hemisphere FW-North America	Lower Lower Lower	ATS-Shuttle-box FTS-Shuttle-box ATS-Horizontal gradient		Schurmann & Steffensen 1992 Schurmann <i>et al.</i> 1991 Bryan <i>et al.</i> 1984
Xenobiotica	<i>Salmo salar</i> <i>Oreochromis mossambicus</i>	ANA-Northern hemisphere FW-Africa	Higher in exposed fish Lower in exposed fish	ATS-Horizontal gradient ATS-Horizontal gradient	DDT in water for 24 hours Copper in water for 8 days	Ogilvie and Anderson 1965 Welch <i>et al.</i> 1989
Season and illumination	<i>Gadus morhua</i> <i>Gadus morhua</i> <i>Gadus morhua</i> <i>Pollachius virens</i> <i>Melanogrammus aeglefinus</i> <i>Boreogadus saida</i> <i>Pomatomus saltatrix</i> <i>Morone saxatilis</i> <i>Petromyzon marinus</i> <i>Gasterosteus aculeatus</i>	M-Atlantic, Arctic M-Atlantic, Arctic M-Atlantic, Arctic M-Atlantic M-Atlantic M-Arctic Ocean M-Atlantic FW-North America, Europe, North Africa ANA-North America, Europe M/FW-Northern hemisphere	Lower Lower during day Lower Lower in winter Lower in winter Lower in winter Lower during night Lower Lower Affected Not affected	FTS-Horizontal gradient Radiotransmitter/field Field surveys FTS-Horizontal gradient FTS-Horizontal gradient FTS-Horizontal gradient FTS-Shuttle-box ATS-Vertical gradient Radiotransmitter/field ATS-Horizontal gradient ATS-Vertical gradient	Juveniles in spring Juveniles in summer Adults in summer Age 1-3 years Juveniles Juveniles in summer Juveniles in autumn Adults in summer, thermal refuges Adults in darkness Collected at different seasons	Clark & Green 1991 Clark & Green 1991 Woodhead & Woodhead 1965 Tatankin 1972 Tatankin 1972 Tatankin 1972 Schurmann & Christiansen 1994 Olla <i>et al.</i> 1985 Moss 1985 McCauley <i>et al.</i> 1977 Røed 1979

res, or (b) fish have been allowed to gravitate to a stable final preferendum over protracted periods of time (usually within 2-3 days). However, differences in experimental methodology are believed to be of minor importance as compared to the effect of nonthermal components (McCauley, 1977; Reynolds and Casterlin, 1979).

TEMPERATURE SELECTION IN CAPELIN AND POLAR COD

This section briefly describes the rationale, objectives and methodology of a current project on biological correlates of selected temperature in capelin and polar cod (Christiansen *et al.*, 1996). Some preliminary results are also presented.

Project rationale and objectives

In contrast to the extreme thermo-stability of Antarctic coastal waters, the temperature of the Arctic Ocean displays seasonal, although small-amplitude, fluctuations. The water body of the Atlantic Ocean meets with the sub-zero waters of the Arctic Basin in the Barents Sea. This results in a thermal gradient that varies in both space and time along the Polar Frontal Zone. Thus, the temperatures of the Barents Sea typically vary between -1.9 and +5°C.

Ecologically, capelin and polar cod are considered to be the piscine key-species inhabiting the Atlantic and the Arctic water bodies, respectively. The zoogeographic distributions of the two species partly overlap in the region of the Polar Frontal Zone. The prognoses regarding the Arctic marine climate suggest that temperature variations will increase, and that the over-all temperature of the Barents Sea decreases (Anon., 1996). Given this scenario, one would expect alterations in migratory behaviour and zoogeographic distribution for the two species. This may have occurred in the waters off West Greenland where polar cod has become increasingly more abundant during the last three decades (Pedersen, 1995). Polar cod might, thus, become a more common species in the central parts of the Barents Sea in the years to come. This, in turn, may have profound consequences for fish, seabirds and mammals which have capelin and polar cod as a major prey (Finley *et al.*, 1990; Haug and Nilssen, 1995; Timoshenko, 1995).

Thermal behaviour in fish has been studied widely but the underlying components assumed to affect temperature selection are still poorly understood. Moreover, few studies have focused on temperature selection in Arctic marine fish (Schurmann and Christiansen, 1994) although one might expect that polar fish species would be more susceptible to environmental temperature changes than their temperate counterparts (Somero and DeVries, 1967; Hoffmann, 1995). Based upon the aforementioned assumptions and ideas, this project intends:

- (1) to focus on a few but fundamental biological components (i.e. ontogeny, sex and sexual maturation, nutritional state, and social interactions) and test how these components affect temperature selection in polar cod and capelin;
- (2) to test final thermal preferenda in captive polar cod from a natural population *vs* artificially raised polar cod which have never experienced sub-zero temperatures. The purpose of this study is to re-examine Fry's "final thermal preferendum" paradigm (Fry, 1947; Reynolds and Casterlin, 1979).

Capelin and polar cod are schooling and shoaling species, respectively, and temperature selection in single fish as well as in smaller groups of fish will be examined using an electronic shuttle-box system (Schurmann and Christiansen, 1994) and a horizontal reversible gradient chamber combined with a time-lapse video-survey. Selectable

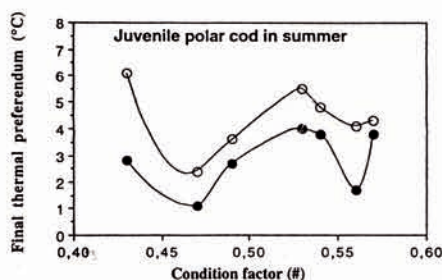


Fig. 1. - Final thermal preferendum vs condition factor for juvenile polar cod in summer. Each individual is represented by a night (filled circle) and day (open circle) value. Circles are interpolated. Note that light conditions do not differ between "night" and "day" due to the midnight sun.

temperatures will range from approximately -1.7 to 15°C for both gradient and shuttle-box devices (Christiansen *et al.*, 1996).

Preliminary results

Final thermal preferenda were determined for seven juvenile polar cod (body size: 10-30 g) using an electronic shuttle-box system. Experiments were conducted in summer in constant light (latitude 70°N). An example of the results is given in figure 1. The condition factor [$= (\text{body weight} \times \text{body length}^{-3})100$] was used as a rough estimate of the nutritional state of the fish.

There were no clear correlation between condition factor and final thermal preferendum. However, there were found to be significant diurnal variations in final preferenda, and fish selected a consistently lower temperature during night (03-09 hours) than during day (15-21 hours) irrespective of condition factor. Diurnal variations in final preferenda may reflect the heterothermal properties of Arctic waters in summer. Given this is so, one would not expect similar variations during the homothermal winter situation where sub-zero temperatures prevail throughout the entire water column.

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Reçu le 20.11.1996.

Accepté pour publication le 20.08.1997.